Plant-Associated Bacteria in Ecosystems Functioning and Sustainability

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1 Introduction

Sustainable crop production will be the fundamental concern of the twenty-first century. Producing adequate food for the world's rising population, renewable energy, and basic molecules in industrial processes all demand increased output. Current agricultural production techniques, for example, inappropriate application of chemical pesticides and fertilizers, have resulted in a slew of human health and environmental issues (Gunnell et al., 2007). New, endemic or re-appearing plant diseases continue to pose a hazard to the development of plant development and health around the world (Miller et al., 2009). Agricultural approaches that are both sound and environmentally benign are becoming increasingly popular. Plant biotechnology has aided in the development of novel crop varieties that are disease resistant, drought and salt tolerant, and nutritionally valuable. Plant-associated microorganisms are usually disregarded in breeding procedures, despite the fact that they conduct critical ecosystem functions for plants and soils. Throughout the last 100 years, however, research has repeatedly proved that microorganisms have an

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intimate relationship with their host plant and are capable of both stimulating plant development and suppressing plant illnesses.

The plant microbiome, which includes the rhizosphere, endosphere, leaf surfaces, and other tissue compartments, can house various bacteria. Plant-associated microbes have been shown to be beneficial in terms of plant health by altering plant physiology, growth, and environmental adaptability/tolerance (Grover et al., 2011; Mendes et al., 2011). Diversified bacterial communities can be found on the surface of seeds, roots, leaves, fruits, as well as vascular tissue, stems, and the intercellular spaces within the plant tissues. All of these bacterial groupings share a number of characteristics that are essential for the host plant's growth promotion.

2 The Phyllosphere

The phyllosphere relates to the above-ground surface of plants as a habitat for microbes. This category includes leaves, stems, blossoms, and fruits. Leaves are the most prevalent tissue for microbial colonization among them. The phyllosphere bacteria interact with the host plant and have the ability to affect the physiology of the host plants.

3 The Spermosphere

The spermosphere is the region surrounding germinating seeds in the soil. It ranges from 1 to 12 mm wide at the soil surface (Schiltz et al., 2015). A multitude of complicated interactions occurs within the spermosphere involving the germinating seed, the soil, and microbes. Many chemicals exuding from seeds impact the microbial populations that live there, either by inhibiting or stimulating their growth (Schiltz et al., 2015).

4 The Rhizosphere

The rhizosphere is the small zone of soil surrounded and impacted by plant roots. It can range in width from 2 to 80 mm from the root surface depending on the plant species. It is the most dynamic and has a substantial impact on the development and the nutritional state of plants (Jones & Hinsinger, 2008; Hinsinger et al., 2009). The presence of root exudates and microbial breakdown products (metabolites), which maintain a diversified and densely populated bacterial population, causes chemical changes in the rhizospheric soil.

Additionally, endophytic sites and vascular tissue are the internal regions of the plant, i.e., epidermis, xylem, and phloem that offer a unique habitat for numerous bacterial communities that have a significant impact on the development of the plants.

Bacteria communities that colonize different regions of plants are divided into epiphytic bacteria which live on the surface, endophytic bacteria which live within the plant tissues, phyllospheric bacteria which nurture on leaf surfaces, and rhizospheric which dwell near the soil. Epiphytic bacteria play a significant role in their host plant's water economy. Beneficial endophytes influence the growth of plants through different mechanisms including hormone synthesis, improved nutrient assimilation, and protection from abiotic/biotic stresses. Numerous studies have reported that endophytic bacteria help in the development of plants such as wheat, rice, canola, potato, tomato, and a variety of other plants (Misko & Germida, 2002; Marquez-Santacruz et al., 2010; Sturz & Nowak, 2000; Mei & Flinn, 2010). For instance, the beneficial endophyte *Paraburkholderia phytofirmans* PsJN, which was isolated from surface-sterilized onion roots and classified as *Pseudomonas* before being reclassified as *Burkholderia* (Sessitsch et al., 2005; Sawana et al., 2014) was able to promote tomato plant growth (Pillay & Nowak, 1997) and upregulated genes involved in signal transduction, protein metabolism, defense pathways, transcription, transport, and hormones metabolism (Galambos et al., 2020). Phyllospheric bacteria provide nutrients the ability to tolerate environmental stress to the host plants. Beneficial rhizospheric bacteria protect plants against pathogens while also aiding in nitrogen fixation. Bacterial communities are associated with plant roots because of the availability of resources such as amino acids, sugars, organic acids, and other small molecules from the plant exudates which can account for up to a third of the carbon fixation of the plants (Whipps, 1990; Bais et al., 2006; Badri et al., 2009; Badri & Vivanco, 2009). Overall, plant-bacterial interactions influence ecosystem functioning in natural ecosystems and agricultural systems through carbon sequestration and nutrient cycling.

Plant Growth-Promoting Bacteria (PGPB)

Soil microorganism can be classified into bacteria, fungi, actinomycetes, protozoa, algae, and nematodes. Majorly, bacterial communities are predominating among the other life forms, accounting for 95% of the total microorganism (10^8 to 10^9 cells/gram of soil). However, the reduced number of bacterial population plummets approx. 10^4 cells/gram is reported under the stressed soil condition (Schoenborn et al., 2004; Timmusk et al., 2011).

Various factors influence the number and type of bacterial load in different soils viz. temperature, moisture content, availability of salt and chemicals, as well as the quantity and varieties of different flora found in such soils (Glick et al., 1999a, 1999b). The interaction of bacteria with plants can be helpful, harmful, or neutral (Lynch, 1990).

Free-living bacteria that are actively involved in specific symbiotic relationships with plants (e.g., *Rhizobia* sp. and *Frankia* sp.), provide positive influence on promoting plant growth. PGPB can influence plant growth either directly by employing resources acquisition or indirectly by reducing the inhibitory effects of some pathogens on plant growth and development, i.e., via biological control of plant pathogenic bacteria or fungi (Glick, 1995).

Historically, *Rhizobia* spp. were extensively studied on the physiological, biochemical, and molecular biological aspects (Dixon & Wheeler, 1986; Fischer, 1994; Long et al., 1982). A vast range of mechanisms has been studied in order to better understand and acknowledge the processes utilized by PCPB (Glick et al., 1999a, 1999b; Glick, 1995; Kloepper et al., 1989). The effect of bacteria on plants may alter because of the variation in the environmental conditions or availability of certain chemicals. The IAA overproducing strain *Pseudomonas fluorescens* BSP53a was capable of stimulating the root development in blackcurrant cuttings while suppressing root development in cherry cuttings (Dubeikovsky et al., 1993).

The following are the mechanism of action:

1. *Direct Mechanism*

PGPB employs a variety of pathways to enhance plant growth and development in a variety of environmental conditions. Biofertilization, phytohormone production, root stimulation, rhizo-remediation, plant stress control, and effective absorption of particular nutrients from the environment are examples of direct mechanisms. Cumulatively, the agricultural soils lack a sufficient number of compounds that led to sub-optimal plant growth. To mitigate these problems, and to attain sufficient plant yields, farmers have extensively utilized chemicals which are the source of nitrogen and phosphorus. Thus, this makes the entire process expensive and poses human health and environmental hazards. Table 1 summarizes the details of the direct mechanism.

Hormones influence a plant's response to the environment, as well as its growth and development (Davies, 2004). During stress or development-limiting environmental conditions, plants strive to modulate their phytohormones to overcome the generated stress (Salamone et al., 2005). A variety of phytohormones promote plant development (Fig. 1).

Table 1 Several direct mechanisms and their role in plant growth development

Types of direct mechanism	Microorganisms	Role	References
Nitrogen fixation	*Azospirillum* sp., *Rhizobia* sp.	Nitrogenase(*nif*) essential genes and required for nitrogen fixation	Bashan and Levanony (1990), James and Olivares (1997)
Solubilization of phosphate	Mycohrrizae	Phosphorus solubilization and mineralization	Richardson (2001), Rodríguez and Fraga (1999)
Sequestering iron	*Pseudomonas* sp.	Low-molecular mass siderophores (approx. 400–1500 Da) and membrane Bacterial species produced receptors that aid in the update of iron	Hider and Kong (2010), Neilands (1981)

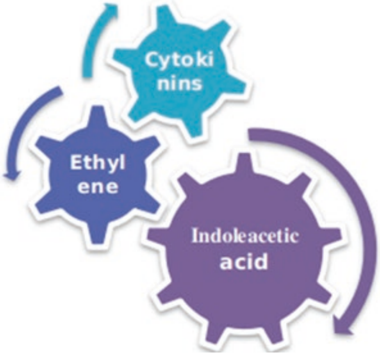

Fig. 1 Essential/several hormones produced by plants

Several strains of *Axontobacter* spp., *Rhizobium* spp., *Pantoea agglomerans, Rhidospirillum rubrum*, *Pseudomonas fluorescens, Bacillus subtilis*, and *Paenibacillus polymyxa* have been reported to produce cytokinins in cell-free medium (Joo et al., 2005; Kang et al., 2009). Indoleacetic acid (IAA) helps in division, expansion, and differentiation of plant cells; triggers the germination of seed and tuber; enhances the rate of xylem and root development; maintains the vegetative growth process; initiates lateral and adventitious root formation; and mediates light, gravity and fluorescence responses. It has an effect/impact on several essential processes, i.e., photosynthesis, pigment production, biosynthesis of different metabolites, and stress tolerance/resistance (Spaepen & Vanderleyden, 2011; Tsavkelova et al., 2006).

Nutrient Uptake

Nitrogen

Nitrogen is a macronutrient that has a fundamental role in plant growth, development, and energy metabolism. Even though the atmospheric N_2 content is 78%, developing plants cannot utilize it. Biological N_2 fixation (BNF) transforms atmospheric N_2 into a form that plant can use by nitrogen-fixing bacteria converting N_2 to NH_3 via a complex enzymatic process known as nitrogenase (Kim & Rees, 1994; Gaby & Buckley, 2012, Rubio & Ludden, 2008, Ahemad & Kibret, 2014 Gómez-Godínez et al., 2019).

Rhizobacteria that promote/enhance plant growth use symbiotic and non-symbiotic ways to fix atmospheric N_2 and make it available to plants. Symbiotic nitrogen-fixing is a mutualistic association between a microbe and a plant. The microorganism penetrated the root and subsequently develops nitrogen-fixing. Plant growth-promoting rhizobacteria, i.e., *Sinorhizobium, Mesorhizobium, Rhizobium*, and *Bradyrhizobium* are commonly found as symbionts in leguminous plants, whereas in non-leguminous shrubs and trees *Frankia* is found (Zahran, 2001).

On the other hand, non-symbiotic nitrogen-fixing bacteria offer a small percentage of the fixed nitrogen required by the bacterially associated host plants. Nitrogen-fixing rhizobial bacteria (a-proteobacteria) family invade and create a symbiotic complex with the roots of leguminous plants. The creation of nodules, in which rhizobia colonize as internal symbionts, is the consequence of a complicated interplay/invade between the host and the symbiont (Giordano & Hirsch, 2004). Diazotrophs are rhizobacteria that promote plant growth by fixing nitrogen in nonleguminous plants and can forma non-obligate association with their hosts (Glick et al., 1999a, 1999b). The nitrogenase complex, a complex enzyme (Kim & Rees, 1994), is responsible for N_2 fixation. Nitrogenase is a metalloenzyme with two components composed of dinitrogenase reductase and dinitrogenase, an iron protein. Dinitrogenase reductase produces a high reducing power electron, which dinitrogenase uses to reduce N_2 to NH_3. Three distinct N-fixing mechanisms have been identified based on the metal cofactors Mo-nitrogenase, Fe-nitrogenase, and V-notrogenase. The major part of biological fixation is completed by molybdenum nitrogenase, which is available and easily accessible in all diazotrophs (Bishop & Joerger, 1990). Nitrogen-fixing genes known as nif genes are reported in both symbiotic and free-living systems (Kim & Rees, 1994). For the formation, creation, and operation of nitrogenase (nif) structural genes, genes involved in Fe, protein activation, iron-molybdenum cofactor biosynthesis, electron donating genes, and regulatory genes all are essential. Nif genes are usually found in a 20–24 kb cluster in diazotrophs, with seven operons synthesizing 20 distinct proteins (Glick, 2012). The molybdenum nitrogenase enzyme complex is composed of two proteins encoded by the nif DK and nifH genes. The NifDK component is a heterotetrameric (a2b2) protein composed of two ab dimers with a 2-fold symmetric connection. One iron-molybdenum cofactor is found inside the active core of each a-subunit (NifD) of NifDK (FeMo-co) (Rubio & Ludden, 2008).

Fix genes, which are found in both free living and symbiotic nitrogen fixation system, governs the symbiotic interaction of nif genes in Rhizobium by requiring low-oxygen condition. (Kim & Rees, 1994). Because nitrogen fixation is an energy-intensive process, microorganisms that fix nitrogen necessitate at least 16 mol of ATP for each mole of lower nitrogen, bacterial carbon resources would be better spent on oxidative phosphorylation, which generates ATP, rather than gluconeogenesis, which generates energy storage capacity of glycogen (Glick, 2012). Treatment of legume plants with rhizobia with a deleted gene for gluconeogenesis resulted in a considerable rise in both the number of nodules and dry weight of plant when compared to the wild-type strain (Zorreguieta et al., 2001).

Phosphate Solubilization

Phosphorus (P), after nitrogen, the second most important macronutrient for plant growth, is abundant in both the forms, i.e., inorganic and organic in soils. Plants have a limited number of possible forms, despite having a vast P reservoir. The majority of soil phosphorus in soil is insoluble, and plants may only acquire it in two soluble forms, dibasic (HPO_2^{-4}) and monobasic ($H_2PO_4{}^{-}$) ions (Bhattacharyya & Jha, 2012; Alaylar et al., 2020). Insoluble P can be observed in both inorganic minerals, such as apatite, and organic forms, like phosphomonoesters, inositol phosphate (soil phytate), and phosphotriesters. To address soil P deficiency, phosphatic fertilizers are commonly applied to agricultural areas. According to Mckenzie and Roberts (1990), plants that can take less phosphatic fertilizers are immediately converted into insoluble complexes in the soil. However, using phosphate fertilizers on a regular basis is quite expensive and non-eco-friendly. As a result, researchers are seeking for an eco-friendly and cost-effective strategy to boost crop yield in low-phosphorus soils.

Phosphate solubilizing microorganisms (PSM) can provide an accessible form of phosphorus to plants, making them a feasible alternative to available chemical phosphatic fertilizers (Khan et al., 2007). Among the several PSM(s) populating the rhizosphere, phosphate-solubilizing bacteria (PSB) are considered potential biofertilizers because they may feed plants with P from sources that are otherwise inaccessible through in a variety of ways (Zaidi et al., 2009). The most important phosphate solubilizing bacteria have been identified as *Microbacterium, Azotobacter, Enterobacter, Rhizobium, Flavobacterium, Microbacterium, Bacillus, Burkholderia, Pseudomonas, Beijerinckia, Sinorhizobium* sp. *RC02, Acinetobacter* sp. *RC04,* and *Serratia* (Bhattacharyya & Jha, 2012; Zhang et al., 2018).

The solubilization of inorganic phosphorus is carried out by the action of low molecular weight organic acids like gluconic and citric acid, produced by a variety of soil bacteria (Zaidi et al., 2009). On the other hand, organic phosphorus is mineralized through the formation of phosphatases that catalyze the hydrolysis of phosphoric esters (Glick, 2012).

Phosphate solubilizing bacteria not only fulfill the requirement of P to plants, but also aid in their growth by increasing the supply of BNF production and availability of other trace minerals. (Suman et al., 2001; Ahmad et al., 2008; Zaidi et al., 2009). Plant growth-promoting rhizobacteria *Pseudomonas auricularis* (HN038) and *Bacillus aryabhattai* (JX285) increase growth, photosynthetic, nutrient uptake, and the production of tea oil (Wu et al., 2019).

Siderophore

Iron (Fe) is an essential component for practically all living things. Except *Lactobacilli* sp., all known bacteria fundamentally require iron (Neilands, 1995) to survive. In aerobic environments, where it is possible to occur insoluble oxyhydroxides and hydroxides can form, iron is mostly found as Fe^{3+}, rendering it reachable to both plants and microbes (Rajkumar et al., 2010). Bacteria obtain iron mostly by the secretion of siderophores, which are low-molecular-mass iron chelating agents. The majority of the siderophores are hydrophilic and can be differentiated into intracellular or extracellular. Rhizobacteria differ regarding the ability to use siderophores supplied by other rhizobacteria of different genera (homologous siderophores), while others can use siderophores generated by other rhizobacteria of other genera (paralogous siderophores) (heterologous siderophores).

In Gram-positive and Gram-negative rhizobacteria, iron (Fe^{3+}) in the Fe^{3+}-siderophore complexes on the bacterial cell membrane is transformed to Fe^{2+}, which is subsequently taken up by the cell from the siderophore via a gated mechanism connecting the inner and outer membranes. During the reduction step, siderophore may be destroyed or recycled (Rajkumar et al., 2010; Neilands, 1995). When there is a lack and shortage of iron, siderophores act as solubilizers for iron from minerals or organic molecules (Indiragandhi et al., 2008).

Plants usually absorb iron from bacteria acquiring different strategies, including chelation and release, direct uptake of siderophore-Fe complexes, and ligand exchange reactions (Schmidt, 1999). Crowley and Kraemer (2007) uncovered a siderophore-mediated iron transport system in oat plants and concluded that rhizosphere bacteria supply iron to oat, which has mechanisms for utilizing Fe-siderophore complexes under iron-limited situations. *Bacillus*, *Azotobacter, Azadirachta, Burkholderia, Rhizobium, Aeromonas*, *Streptomyces* sp., *Pseudomonas, Serratia,* and other plant growth-promoting rhizobacteria have been demonstrated to take up radiolabeled ferric siderophores as a sole source of iron. Similarly, *Arabidopsis thaliana* plants absorbed the Fe-pyoverdine complex produced by *Pseudomonas fluorescens* C7, due to the increase in iron in plant tissues and increased plant growth (Vansuyt et al., 2007). In *Zea mays,* the effect of the siderophore-producing *Pseudomonas* strain GRP3 was studied. After 45 days, chlorotic symptoms diminished, and iron, chlorophyll a, and chlorophyll b levels rose in strain GRP3 infected plants, compared to control plants (Sharma & Johri, 2003).

Potassium

Potassium (K) is the highly important third most macronutrient for plant growth. Soluble potassium concentrations in soil are typically low, and more than 90% of potassium in the soil is in the form of insoluble rocks and silicate minerals. As a result of unbalanced fertilizer application, potassium deficiency is becoming one of the most significant constraints to crop productivity. Plants with low potassium levels will have underdeveloped roots, continue growing, generate small seeds, and produce inferior yields. This emphasized the importance of finding an alternative native source of potassium for plant root uptake and maintaining potassium levels in soils for agricultural output sustainability.

Plant growth-promoting rhizobacteria are capable of dissolving potassium rock through the production and release of organic acids. *Paenibacillus* sp., *Burkholderia, Acidothiobacillus ferrooxidans, B. edaphicus, Pseudomonas,* and *B. mucilaginosus* have all been found to create potassium in a viable form from potassium-containing minerals in soils. As a result, adopting potassium-solubilizing plant growth-promoting rhizobacteria as a biofertilizer for agriculture development can serve to minimize the usage of agrochemicals while also encouraging sustainable crop production (Kang et al., 2017).

Phytohormone

A variety of microorganisms live in the rhizosphere, and they can produce compounds that govern plant growth and development. Plant growth-promoting rhizobacteria produce auxins, gibberellins, cytokinins, and ethylene which can impact cell proliferation in the root architecture by producing an excessive production of lateral roots and root hairs, resulting in an increase in nutrition and water intake.

IAA Production

Indole acetic acid (IAA) is the most common natural auxin present in plants and has a beneficial effect on root growth. Up to 80% of rhizobacteria colonized the seed or root surfaces can produce indole acetic acid (IAA), which is thought to work in concert with endogenous IAA in plants to increase cell growth and improve the host's absorption of minerals and nutrients from the soil. IAA stimulated plant cell elongation, division and differentiation; root development and increases xylem content, adventitious and lateral root formation, influences photosynthesis, induces seed and tuber germination; controls vegetative growth processes; regulates responses to gravity, light, and florescence; formation of both shoot and root apical meristems (Kepinski, 2006; Casimiro et al., 2001; Sachs, 2005). In bacteria, tryptophan, an amino acid typically found in root exudates, has been identified as the primary precursor molecule for IAA production (Zhao, 2010). In bacteria like *Rhizobium, Klebsiella, Bradyrhizobium, Pseudomonas, Agrobacterium*, and *Enterobacterium,* the synthesis of indole acetic acid involves the generation of indole-3-pyruvic acid and indole-3-acetic aldehyde, chemically synthesized hormones are considered less effective as they have a poor tolerance between suppressive and stimulatory levels, but microbial hormones have a higher tolerance due to their continuous slow release.

Ethylene

Ethylene is a key phytohormone that affects plant growth and development in a variety of ways, that includes lateral bud development, root initiation and elongation, promoting fruit ripening, anthocyanin synthesis, promoting lower drooping, enhanced seed germination, promoting leaf abscission, and the synthesis of volatile compounds responsible for aroma in fruits are all enhanced by ethylene. High ethylene concentrations cause defoliation and other cellular functions, which may result in decreased crop productivity (Bleecker & Kende, 2000). The 1-aminocyclopropane-1 carboxylic acid (ACC), which is a direct precursor of ethylene, is catalyzed by ACC oxidase.

ACC deaminase is an enzyme that catalysis the hydrolytic cleavage of ACC thus inhibiting ethylene production. *Pseudomonas* sp. that consists of ACC deaminase along with *R. leguminosarum* was found to enhance fresh biomass, straw yield, grain yield, nodule dry weight, nodule number, and nutrient uptake in lentil grains as a result of lowering ethylene production (Kaneko et al., 2002; Ma et al., 2003). *Burkholderia*, *Rhizobium*, *Pseudomonas*, *Agrobacterium*, *Ralstonia*, *Azospirillum*, *Acinetobacte*r, *Serratia*, *Achromobacter, Alcaligenes, Bacillus, Burkholderia,* and *Enterobacter* are among others that have ACC deaminase-producing bacteria (Table 2).

2. *Indirect Mechanism*

   The use of biocontrol bacteria that indirectly boost plant development has piqued curiosity since it uses bacteria instead of chemical pesticides. Induced systemic resistance (ISR), antifungal and antibacterial production by PGPB are examples of indirect methods which are effective in plant protection (Kloepper & Schroth, 1981; Egamberdieva & Lugtenberg, 2014). The following is a list of compounds and hormones that underlie this category (Compant et al., 2005).

   2.1 *Production of compounds with antibiotic and lytic activity:* Beneficial bacterial such as PGPB produce antibacterial and numerous other metabolites

Table 2 Different types of rhizobacteria and their functions

Rhizobacteria	Crop	Function	References
Sphingomonas	Tomato	Gibberellin synthesis	Khan et al. (2014)
Chryseobacterium	Tomato	Siderophore production (Increase soil microbial biomass)	Radzki et al. (2013)
Azotobacter	Wheat, tobacco, maize, coffee	Nitrogen fixation	Wani et al. (2013)
Phyllobacterium	Strawberry	Potassium and phosphate	Flores-Félix et al. (2018)
Pseudomonas	Mung bean	ACC deaminase synthesis	Ahmad et al. (2013)
Bacillus sp. JC03, *E. coli* DH5α	*A .thaliana*	Strigolactones production	Jiang et al. (2019)
C. zhacaiensis, B. amyloliquefaciens	Tomato	Cytokinin production	Selvakumar et al. (2018)
Stenotrophomonas maltophilia	Wheat	Nitrogenase activity, P-solubilization, IAA, ACC deaminase	Verma et al. (2014a, b)
Paenibacillus mucilaginosus	Soybean	Potassium and phosphate solubilization	Ma et al. (2018)
Bradyrhizobium diazoefficiens USDA110	Soybean	Nitrogen fixation	Sibponkrung et al. (2020)
Rahnella aquatilis (PGP30), *Pseudomonas brassicacearum* (PGP291), *Rhizobium* sp. (RhOF57A)	Faba bean	Phosphate, potassium solubilization, nitrogen fixation, EPS production	Bechtaoui et al. (2020)
Sinorhizobium sp. RC02, *Acinetobacter* sp. RC04	Safflower	Phosphorous solubilization, promote seed germination	Zhang et al. (2018)
Bacillus aryabhattai (JX285) and *Pseudomonas auricularis* (HN038)	*Camellia oleifera* Abel.	Solubilization of phosphate increases growth, photosynthesis, yield, and increases tea oil	Wu et al. (2019)
Azospirillum	Maize	Nitrogen fixation	Gómez-Godínez et al. (2019)

that play a crucial role in the protection of plant from the plant pathogen especially fungus (Haas & Keel, 2003; Mazurier et al., 2009). Also, some of the enzymes secreted by the biocontrol bacteria have the ability to lyse the cell walls of *Fusarium oxysporum, Phytophthora* spp., *Rhizoctonia solani*, and *Pythium ultimum,* all of which are considered as pathogenic fungi (Frankowski et al., 2001; Kim et al., 2008).

2.2 *Siderophores:* Some bacterial species, on the other hand can act as biocontrol agents through the development of siderophores. Siderophores from PGPB can block phytopathogens from acquiring iron, restricting their growth (Siebner-Freibach et al., 2003).

2.3 *Plant-induced systemic resistance:* Plant growth-promoting bacteria can activate the resistance in plants by a process known as induced systemic resistance (ISR), in which plants' defense system is activated against infection caused by the pathogen. The ISR-positive plants are also known as "primed" due to their tendency to react and respond quickly and strongly against the pathogenic attack (Pieterse et al., 2009).

3. *Modulating the Stress Impacts of Environmental Conditions*

Ideally, a major part of the plant growth and development would be thought to be linearly decreasing over the period of time (Glick et al., 2007). However, in the natural environment, a large number of biotic and abiotic stresses can stifle the growth of the plant. Among them are extreme temperature, intensity of light, flood, drought, toxic metals and organic pollutants, radiation, injury, insect attack, nematode infection, high salinity, metal and metalloids, hypoxia, and various pathogens such as disease-causing viruses, bacteria, and fungi (Mayak et al., 2004).

Many environmental stresses such as phytopathogenic infection may lead to the production of the inhibitory stress hormone ethylene (Glick, 2004). Studies have shown that many ACC deaminase-producing PGPB have the ability to protect the plants from abiotic stresses (Reed & Glick, 2005).

In addition, it has been reported that PGPB may help plants in mitigating abiotic stresses by synthesizing indoleacetic acid (IAA) that facilitates the growth and development of the plant in the presence of growth-inhibiting compounds (Wani et al., 2008).

According to one study, the IAA and ACC deaminase mechanisms work synergistically to enhance plant growth (Gamalero & Glick, 2010; Salamone et al., 2005). Plants roots exudate consist of an amino acid known as tryptophan. PGPB converts the tryptophan present in the soil to IAA. The IAA produced by bacteria is released and absorbed by the plant cells which results in the activation of the auxin signaling pathway, which is comprised of several auxin-responsive factors and the plants' IAA pool (Fig. 2). IAA absorption leads to cell growth and proliferation of the plant. Simultaneously, few IAAs activate the transcription machinery that leads to the transcription of the gene encoding the enzyme ACC synthase. Production of ACC synthase increases the levels of ACC and ultimately ethylene (ACC is the precursor of ethylene which is catalyzed by the enzyme ACC oxidase into ethylene).

In addition to IAA, cytokinins (compounds with an adenine-like structure) can stimulate cytokinesis, or cell division. Cytokinins are produced by several yeast strains, and by a number of soil bacteria, including PGPB (Salamone et al., 2001). Transgenic plants that are developed to overproduce the cytokinins during abiotic stress have been shown to effectively tolerate the negative impacts of environmental challenges (Stearns et al., 2012).

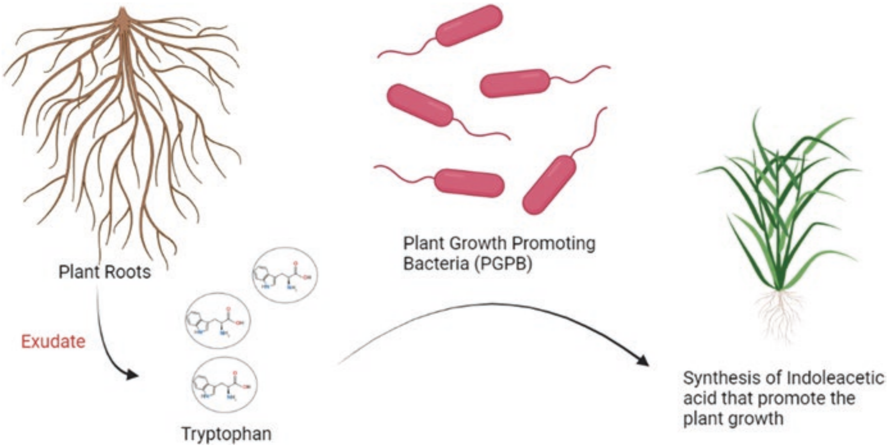

Fig. 2 Representation of PGPB role in converting the tryptophan into IAA for plant proliferation

Another compound, Trehalose, a non-reducing disaccharide, α, α-1,1-glucoside, comprises two molecules glucose and fructose that are extensively found in nature. It is found in bacteria, yeast, fungi, plants, insects, and invertebrates. Trehalose can provide plants protection against drought, excessive salt, and harsh temperatures. This compound is a highly stable metabolite that is resistant to acids and high temperatures and when cells dry up, it can form a gel phase, which replaces water and reduces drought and salt damage (Rivero et al., 2007).

Challenges

Despite the fact that bacteria are being utilized effectively in many developing countries for crop protection and production, there are still certain limitations/challenges that exist in the terms of the widespread adoption of the plant growth-promoting bacteria. For example, a number of unique methods have to be developed for bacteria growth, storage, shipping, formulation, and application while moving the studies done in laboratory and greenhouses to field trials and large-scale commercial fields. Secondly, the general public must be made aware of the widespread use of these beneficial bacteria in agricultural fields. Before the general public accepts the widespread discharge of growth-promoting bacteria into the environment, the myth must be dispelled that limits the microorganisms to their role as pathogens.

References

Ahemad, M., & Kibret, M. (2014). Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective. *Journal of King Saud University-Science, 26*(1), 1–20.

Ahmad, F., Ahmad, I., & Khan, M. S. (2008). Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities. *Microbiological Research, 163*(2), 173–181.

Ahmad, M., Zahir, Z. A., Nazli, F., Akram, F., Arshad, M., & Khalid, M. (2013). Effectiveness of halo-tolerant, auxin producing Pseudomonas and Rhizobium strains to improve osmotic stress tolerance in mung bean (Vigna radiata L.). *Brazilian Journal of Microbiology, 44*, 1341–1348.

Alaylar, B., Egamberdieva, D., Gulluce, M., Karadayi, M., & Arora, N. K. (2020). Integration of molecular tools in microbial phosphate solubilization research in agriculture perspective. *World Journal of Microbiology and Biotechnology, 36*(7), 1–12.

Badri, D. V., & Vivanco, J. M. (2009). Regulation and function of root exudates. *Plant, Cell and Environment, 32*(6), 666–681.

Badri, D. V., Weir, T. L., van der Lelie, D., & Vivanco, J. M. (2009). Rhizosphere chemical dialogues: Plant-microbe interactions. *Current Opinion in Biotechnology, 20*(6), 642–650.

Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S., & Vivanco, J. M. (2006). The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology, 57*, 233–266.

Bashan, Y., & Levanony, H. (1990). Current status of Azospirillum inoculation technology: Azospirillum as a challenge for agriculture. *Canadian Journal of Microbiology, 36*(9), 591–608.

Bechtaoui, N., Raklami, A., Benidire, L., Tahiri, A. I., Göttfert, M., & Oufdou, K. (2020). Effects of PGPR co-inoculation on growth, phosphorus nutrition and phosphatase/phytase activities of faba bean under different phosphorus availability conditions. *Polish Journal of Environmental Studies, 29*(2), 1557–1565.

Bhattacharyya, P. N., & Jha, D. K. (2012). Plant growth-promoting rhizobacteria (PGPR): Emergence in agriculture. *World Journal of Microbiology and Biotechnology, 28*(4), 1327–1350.

Bishop, P. E., & Joerger, R. D. (1990). Genetics and molecular biology of alternative nitrogen fixation systems. *Annual Review of Plant Biology, 41*(1), 109–125.

Bleecker, A. B., & Kende, H. (2000). Ethylene: A gaseous signal molecule in plants. *Annual Review of Cell and Developmental Biology, 16*(1), 1–18.

Casimiro, I., Marchant, A., Bhalerao, R. P., Beeckman, T., Dhooge, S., Swarup, R., et al. (2001). Auxin transport promotes Arabidopsis lateral root initiation. *The Plant Cell, 13*(4), 843–852.

Compant, S., Duffy, B., Nowak, J., Clément, C., & Ait Barka, E. (2005). Use of plant growth-promoting bacteria for biocontrol of plant diseases: Principles, mechanisms of action, and future prospects. *Applied and Environmental Microbiology, 71*(9), 4951–4959.

Crowley, D. E., & Kraemer, S. M. (2007). 7 Function of siderophores. In *The rhizosphere: Biochemistry and organic substances at the soil-plant interface* p. 173.

Davies, P. J. (2004). *Plant hormones: Biosynthesis, signal transduction, action!* Kluwer Academic.

Dixon, R. O. D., & Wheeler, C. T. (1986). *Nitrogen fixation in plants*. Blackie and Son.

Dubeikovsky, A. N., Mordukhova, E. A., Kochetkov, V. V., Polikarpova, F. Y., & Boronin, A. M. (1993). Growth promotion of blackcurrant softwood cuttings by recombinant strain *Pseudomonas fluorescens* BSP53a synthesizing an increased amount of indole-3-acetic acid. *Soil Biology and Biochemistry, 25*(9), 1277–1281.

Egamberdieva, D., & Lugtenberg, B. (2014). Use of plant growth-promoting rhizobacteria to alleviate salinity stress in plants. In *Use of microbes for the alleviation of soil stresses* (Vol. 1, pp. 73–96). Springer.

Fischer, H. M. (1994). Genetic regulation of nitrogen fixation in rhizobia. *Microbiological Reviews, 58*(3), 352–386.

Flores-Félix, J. D., Velázquez, E., García-Fraile, P., González-Andrés, F., Silva, L. R., & Rivas, R. (2018). Rhizobium and Phyllobacterium bacterial inoculants increase bioactive compounds and quality of strawberries cultivated in field conditions. *Food Research International, 111*, 416–422.

Frankowski, J., Lorito, M., Scala, F., Schmid, R., Berg, G., & Bahl, H. (2001). Purification and properties of two chitinolytic enzymes of Serratia plymuthica HRO-C48. *Archives of Microbiology, 176*(6), 421–426.

Gaby, J. C., & Buckley, D. H. (2012). A comprehensive evaluation of PCR primers to amplify the nifH gene of nitrogenase. *PLoS ONE, 7*(7), e42149.

Galambos, N., Compant, S., Moretto, M., Sicher, C., Puopolo, G., Wäckers, F., Sessitsch, A., Pertot, I., & Perazzolli, M. (2020). Humic acid enhances the growth of tomato promoted by endophytic bacterial strains through the activation of hormone-, growth-, and transcription-related processes. *Frontiers in Plant Science, 11*(September), 582267.

Gamalero, E., & Glick, B. R. (2010). Bacterial ACC deaminase and IAA: Interactions and consequences for plant growth in polluted environments. In I. A. Golubev (Ed.), *Handbook of phytoremediation* (pp. 763–774). Nova Science.

Giordano, W., & Hirsch, A. M. (2004). The expression of MaEXP1, a Melilotus alba expansin gene, is upregulated during the sweetclover-Sinorhizobium meliloti interaction. *Molecular Plant-Microbe Interactions, 17*(6), 613–622.

Glick, B. R. (1995). The enhancement of plant growth by free-living bacteria. *Canadian Journal of Microbiology, 41*(2), 109–117.

Glick, B. R. (2004). Bacterial ACC deaminase and the alleviation of plant stress. *Advances in Applied Microbiology, 56*, 291–312.

Glick, B. R. (2012). Plant growth-promoting bacteria: Mechanisms and applications. *Scientifica, 2012*, 963401.

Glick, B. R., Patten, C. L., Holguin, G., & Penrose, D. M. (1999a). *Biochemical and genetic mechanisms used by plant growth promoting bacteria*. Imperial College Press.

Glick, B. R., Patten, C., Holguin, G., & Penrose, D. (1999b). Overview of plant growth-promoting bacteria. In *Biochemical and genetic mechanisms used by plant growth promoting bacteria* (pp. 1–13). Imperial College Press.

Glick, B. R., Cheng, Z., Czarny, J., & Duan, J. (2007). Promotion of plant growth by ACC deaminase-producing soil bacteria. *European Journal of Plant Pathology, 119*(3), 329–339.

Gómez-Godínez, L. J., Fernandez-Valverde, S. L., Romero, J. C. M., & Martínez-Romero, E. (2019). Metatranscriptomics and nitrogen fixation from the rhizoplane of maize plantlets inoculated with a group of PGPRs. *Systematic and Applied Microbiology, 42*(4), 517–525.

Grover, M., Ali, S. Z., Sandhya, V., Rasul, A., & Venkateswarlu, B. (2011). Role of microorganisms in adaptation of agriculture crops to abiotic stresses. *World Journal of Microbiology and Biotechnology.* https://doi.org/10.1007/s11274-010-0572-7.

Gunnell, D., Eddleston, M., Phillips, M. R., & Konradsen, F. (2007). The global distribution of fatal pesticide self-poisoning: Systematic review. *BMC Public Health, 7*(December), 357.

Haas, D., & Keel, C. (2003). Regulation of antibiotic production in root-colonizing Pseudomonas spp. and relevance for biological control of plant disease. *Annual Review of Phytopathology, 41*, 117–153.

Hider, R. C., & Kong, X. (2010). Chemistry and biology of siderophores. *Natural Product Reports, 27*(5), 637–657.

Hinsinger, P., Glyn Bengough, A., Vetterlein, D., & Young, I. M. (2009). Rhizosphere: Biophysics, biogeochemistry and ecological relevance. *Plant and Soil.* https://doi.org/10.1007/s11104-008-9885-9.

Indiragandhi, P., Anandham, R., Madhaiyan, M., Kim, G. H., & Sa, T. (2008). Cross-utilization and expression of outer membrane receptor proteins for siderophore uptake by Diamondback moth Plutella xylostella (Lepidoptera: Plutellidae) gut bacteria. *FEMS Microbiology Letters, 289*(1), 27–33.

James, E. K., & Olivares, F. L. (1997). Infection and colonization of sugar cane and other graminaceous plants by endophytic diazotrophs. *Critical Reviews in Plant Sciences, 17*(1), 77–119.

Jiang, C. H., Xie, Y. S., Zhu, K., Wang, N., Li, Z. J., Yu, G. J., & Guo, J. H. (2019). Volatile organic compounds emitted by Bacillus sp. JC03 promote plant growth through the action of auxin and strigolactone. *Plant Growth Regulation, 87*(2), 317–328.

Jones, D. L., & Hinsinger, P. (2008). The rhizosphere: Complex by design. *Plant and Soil.* https://doi.org/10.1007/s11104-008-9774-2.

Joo, G. J., Kim, Y. M., Kim, J. T., Rhee, I. K., Kim, J. H., & Lee, I. J. (2005). Gibberellins-producing rhizobacteria increase endogenous gibberellins content and promote growth of red peppers. *Journal of Microbiology, 43*(6), 510–515.

Kaneko, T., Nakamura, Y., Sato, S., Minamisawa, K., Uchiumi, T., Sasamoto, S., et al. (2002). Complete genomic sequence of nitrogen-fixing symbiotic bacterium Bradyrhizobium japonicum USDA110. *DNA Research, 9*(6), 189–197.

Kang, S. M., Joo, G. J., Hamayun, M., et al. (2009). Gibberellin production and phosphate solubilization by newly isolated strain of Acinetobacter calcoaceticus and its effect on plant growth. *Biotechnology Letters, 31*(2), 277–281.

Kang, S. M., Waqas, M., Shahzad, R., You, Y. H., Asaf, S., Khan, M. A., et al. (2017). Isolation and characterization of a novel silicate-solubilizing bacterial strain Burkholderia eburnea CS4-2 that promotes growth of japonica rice (Oryza sativa L. cv. Dongjin). *Soil Science and Plant Nutrition, 63*(3), 233–241.

Kepinski, S. (2006). Integrating hormone signaling and patterning mechanisms in plant development. *Current Opinion in Plant Biology, 9*(1), 28–34.

Khan, M. S., Zaidi, A., & Wani, P. A. (2007). Role of phosphate-solubilizing microorganisms in sustainable agriculture—A review. *Agronomy for Sustainable Development, 27*(1), 29–43.

Khan, A. L., Waqas, M., Kang, S. M., Al-Harrasi, A., Hussain, J., Al-Rawahi, A., et al. (2014). Bacterial endophyte Sphingomonas sp. LK11 produces gibberellins and IAA and promotes tomato plant growth. *Journal of Microbiology, 52*(8), 689–695.

Kim, J., & Rees, D. C. (1994). Nitrogenase and biological nitrogen fixation. *Biochemistry, 33*(2), 389–397.

Kim, Y. C., Jung, H., Kim, K. Y., & Park, S. K. (2008). An effective biocontrol bioformulation against Phytophthora blight of pepper using growth mixtures of combined chitinolytic bacteria under different field conditions. *European Journal of Plant Pathology, 120*(4), 373–382.

Kloepper, J. W., & Schroth, M. N. (1981). Relationship of in vitro antibiosis of plant growth promoting rhizobacteria to plant growth and the displacement of root microflora. *Phytopathology, 71*, 1020–1024.

Kloepper, J. W., Lifshitz, R., & Zablotowicz, R. M. (1989). Free-living bacterial inocula for enhancing crop productivity. *Trends in Biotechnology, 7*(2), 39–44.

Long, S. R., Buikema, W. J., & Ausubel, F. M. (1982). Cloning of Rhizobium meliloti nodulation genes by direct complementation of Nod− mutants. *Nature, 298*(5873), 485–488.

Lynch, J. M. (Ed.). (1990). *The Rhizosphere*. Wiley-Interscience.

Ma, W., Guinel, F. C., & Glick, B. R. (2003). Rhizobium leguminosarum biovar viciae 1-aminocyclopropane-1-carboxylate deaminase promotes nodulation of pea plants. *Applied and Environmental Microbiology, 69*(8), 4396–4402.

Ma, M., Jiang, X., Wang, Q., Guan, D., Li, L., Ongena, M., & Li, J. (2018). Isolation and identification of PGPR strain and its effect on soybean growth and soil bacterial community composition. *International Journal of Agriculture and Biology, 20*, 1289–1297.

Marquez-Santacruz, H. A., Hernandez-Leon, R., Orozco-Mosqueda, M. C., Velazquez-Sepulveda, I., & Santoyo, G. (2010). Diversity of bacterial endophytes in roots of Mexican Husk tomato plants (Physalis Ixocarpa) and their detection in the rhizosphere. *Genetics and Molecular Research.* https://doi.org/10.4238/vol9-4gmr921.

Marroquı, S., Zorreguieta, A., Santamaría, C., Temprano, F., Soberón, M., Megías, M., & Downie, J. A. (2001). Enhanced symbiotic performance by Rhizobium tropici glycogen synthase mutants. *Journal of Bacteriology, 183*(3), 854–864.

Mayak, S., Tirosh, T., & Glick, B. R. (2004). Plant growth-promoting bacteria that confer resistance to water stress in tomatoes and peppers. *Plant Science, 166*(2), 525–530.

Mazurier, S., Corberand, T., Lemanceau, P., & Raaijmakers, J. M. (2009). Phenazine antibiotics produced by fluorescent pseudomonads contribute to natural soil suppressiveness to Fusarium wilt. *ISME Journal, 3*(8), 977–991.

McKenzie, R. H., & Roberts T. L. (1990). Soil and fertilizers phosphorus update. In *Proc. Alberta soil science workshop proceedings, Edmonton, Alberta. Feb. 20–22* (pp. 84–104)

Mei, C., & Flinn, B. S. (2010). The use of beneficial microbial endophytes for plant biomass and stress tolerance improvement. *Recent Patents on Biotechnology, 4*(1), 81–95.

Mendes, R., Kruijt, M., de Bruijn, I., Dekkers, E., van der Voort, M., Schneider, J. H. M., Piceno, Y. M., et al. (2011). Deciphering the rhizosphere microbiome for disease-suppressive bacteria. *Science, 332*(6033), 1097–1100.

Miller, S. A., Beed, F. D., & Harmon, C. L. (2009). Plant disease diagnostic capabilities and networks. *Annual Review of Phytopathology, 47*, 15–38.

Misko, A. L., & Germida, J. J. (2002). Taxonomic and functional diversity of pseudomonads isolated from the roots of field-grown Canola. *FEMS Microbiology Ecology, 42*(3), 399–407.

Neilands, J. B. (1981). Iron absorption and transport in microorganisms. *Annual Review of Nutrition, 1*, 27–46.

Neilands, J. B. (1995). Siderophores: Structure and func-tion of microbial iron transport compounds. *The Journal of Biological Chemistry, 270*, 26723–26726.

Pieterse, C. M. J., Leon-Reyes, A., van der Ent, S., & van Wees, S. C. M. (2009). Networking by small-molecule hormones in plant immunity. *Nature Chemical Biology, 5*(5), 308–316.

Pillay, V. K., & Nowak, J. (1997). Inoculum density, temperature, and genotype effects on in vitro growth promotion and epiphytic and endophytic colonization of tomato (Lycopersicon Esculentum L.) seedlings inoculated with a pseudomonad bacterium. *Canadian Journal of Microbiology.* https://doi.org/10.1139/m97-049.

Radzki, W., Mañero, F. G., lgar, E., García, J. L., García-Villaraco, A., Solano, B. R. (2013). Bacterial siderophores efficiently provide iron to iron-starved tomato plants in hydroponics culture. *Antonie Van Leeuwenhoek, 104*, 321–330.

Rajkumar, M., Ae, N., Prasad, M. N. V., & Freitas, H. (2010). Potential of siderophore-producing bacteria for improving heavy metal phytoextraction. *Trends in Biotechnology, 28*(3), 142–149.

Reed, M. L. E., & Glick, B. R. (2005). Growth of canola (Brassica napus) in the presence of plant growth-promoting bacteria and either copper or polycyclic aromatic hydrocarbons. *Canadian Journal of Microbiology, 51*(12), 1061–1069.

Richardson, A. E. (2001). Prospects for using soil microorganisms to improve the acquisition of phosphorus by plants. *Functional Plant Biology, 28*(9), 897–906.

Rivero, R. M., Kojima, M., Gepstein, A., et al. (2007). Delayed leaf senescence induces extreme drought tolerance in a flowering plant. *Proceedings of the National Academy of Sciences of the United States of America, 104*(49), 19631–19636.

Rodríguez, H., & Fraga, R. (1999). Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances, 17*(4–5), 319–339.

Rubio, L. M., & Ludden, P. W. (2008). Biosynthesis of the iron-molybdenum cofactor of nitrogenase. *Annual Review of Microbiology, 62*, 93.

Sachs, T. (2005). Auxin's role as an example of the mechanisms of shoot/root relations. *Plant and Soil, 268*(1), 13–19.

Salamone, I. E. G., Hynes, R. K., & Nelson, L. M. (2001). Cytokinin production by plant growth promoting rhizobacteria and selected mutants. *Canadian Journal of Microbiology, 47*(5), 404–411.

Salamone, I. E. G., Hynes, R. K., & Nelson, L. M. (2005). Role of cytokinins in plant growth promotion by rhizosphere bacteria. In Z. A. Siddiqui (Ed.), *PGPR: Biocontrol and biofertilization* (pp. 173–195). Springer.

Sawana, A., Adeolu, M., & Gupta, R. S. (2014). Molecular signatures and phylogenomic analysis of the genus Burkholderia: Proposal for division of this genus into the emended genus Burkholderia containing pathogenic organisms and a new genus Paraburkholderia Gen. Nov. Harboring environmental species. *Frontiers in Genetics.* https://doi.org/10.3389/fgene.2014.00429.

Schiltz, S., Gaillard, I., Pawlicki-Jullian, N., Thiombiano, B., Mesnard, F., & Gontier, E. (2015). A review: What is the spermosphere and how can it be studied? *Journal of Applied Microbiology, 119*(6), 1467–1481.

Schmidt, W. (1999). Mechanisms and regulation of reduction-based iron uptake in plants. *The New Phytologist, 141*(1), 1–26.

Schoenborn, L., Yates, P. S., Grinton, B. E., Hugenholtz, P., & Janssen, P. H. (2004). Liquid serial dilution is inferior to solid media for isolation of cultures representative of the phylum-level diversity of soil bacteria. *Applied and Environmental Microbiology, 70*(7), 4363–4366.

Selvakumar, G., Bindu, G. H., Bhatt, R. M., Upreti, K. K., Paul, A. M., Asha, A., et al. (2018). Osmotolerant cytokinin producing microbes enhance tomato growth in deficit irrigation conditions. *Proceedings of the National Academy of Sciences, India Section B: Biological Sciences, 88*(2), 459–465.

Sessitsch, A., Coenye, T., Sturz, A. V., Vandamme, P., Ait Barka, E., Salles, J. F., Van Elsas, J. D., et al. (2005). Burkholderia Phytofirmans Sp. Nov., a Novel plant-associated bacterium with plant-beneficial properties. *International Journal of Systematic and Evolutionary Microbiology.* https://doi.org/10.1099/ijs.0.63149-0.

Sharma, A., & Johri, B. N. (2003). Growth promoting influence of siderophore-producing pseudomonas strains GRP3A and PRS9 in maize (Zea mays L.) under iron limiting conditions. *Microbiological Research, 158*(3), 243–248.

Sibponkrung, S., Kondo, T., Tanaka, K., Tittabutr, P., Boonkerd, N., Yoshida, K. I., & Teaumroong, N. (2020). Co-inoculation of Bacillus velezensis strain S141 and Bradyrhizobium Strains promotes nodule growth and nitrogen fixation. *Microorganisms, 8*(5), 678.

Siebner-Freibach, H., Hadar, Y., & Chen, Y. (2003). Siderophores sorbed on Ca-montmorillonite as an iron source for plants. *Plant and Soil, 251*(1), 115–124.

Spaepen, S., & Vanderleyden, J. (2011). Auxin and plant-microbe interactions. *Cold Spring Harbor Perspectives in Biology, 3*(4), a001438.

Stearns, J. C., Woody, O. Z., McConkey, B. J., & Glick, B. R. (2012). Effects of bacterial ACC deaminase on Brassica napus gene expression measured with an Arabidopsis thaliana microarray. *Molecular Plant-Microbe Interactions, 25*, 668–676.

Sturz, A. V., & Nowak J.. (2000). Endophytic communities of Rhizobacteria and the strategies required to create yield enhancing associations with crops. *Applied Soil Ecology.* https://doi.org/10.1016/s0929-1393(00)00094-9.

Suman, A., Shasany, A. K., Singh, M., Shahi, H. N., Gaur, A., & Khanuja, S. P. S. (2001). Molecular assessment of diversity among endophytic diazotrophs isolated from subtropical Indian sugarcane. *World Journal of Microbiology and Biotechnology, 17*(1), 39–45.

Timmusk, S., Paalme, V., Pavlicek, T., et al. (2011). Bacterial distribution in the rhizosphere of wild barley under contrasting microclimates. *PLoS One, 6*(3), Article ID e17968.

Tsavkelova, E. A., Klimova, S. Y., Cherdyntseva, T. A., & Netrusov, A. I. (2006). Microbial producers of plant growth stimulators and their practical use: A review. *Applied Biochemistry and Microbiology, 42*(2), 117–126.

Vansuyt, G., Robin, A., Briat, J. F., Curie, C., & Lemanceau, P. (2007). Iron acquisition from Fe-pyoverdine by Arabidopsis thaliana. *Molecular Plant-Microbe Interactions, 20*(4), 441–447.

Verma, J. P., Yadav, J., Tiwari, K. N., & Jaiswal, D. K. (2014a). Evaluation of plant growth promoting activities of microbial strains and their efect on growth and yield of chickpea (Cicer arietinum L.) in India. *Soil Biology and Biochemistry, 70*, 33–37.

Verma, P., Yadav, A. N., Kazy, S. K., Saxena, A. K., & Suman, A. (2014b). Evaluating the diversity and phylogeny of plant growth promoting bacteria associated with wheat (Triticum aestivum) growing in central zone of India. *International Journal of Current Microbiology and Applied Science, 3*(5), 432–447.

Wani, P. A., Khan, M. S., & Zaidi, A. (2008). Effect of metal-tolerant plant growth-promoting Rhizobium on the performance of pea grown in metal-amended soil. *Archives of Environmental Contamination and Toxicology, 55*(1), 33–42.

Wani, S. A., Chand, S., & Ali, T. (2013). Potential use of Azotobacter chroococcum in crop production: an overview. *Current Agriculture Research Jornal, 1*(1), 35–38.

Whipps, J. M. (1990). Carbon utilization. In J. M. Lynch (Ed.), *The rhizosphere* (pp. 59–97). Wiley-Interscience.

Wu, F., Li, J., Chen, Y., Zhang, L., Zhang, Y., Wang, S., et al. (2019). Effects of phosphate solubilizing bacteria on the growth, photosynthesis, and nutrient uptake of Camellia oleifera Abel. *Forests, 10*(4), 348.

Zahran, H. H. (2001). Rhizobia from wild legumes: Diversity, taxonomy, ecology, nitrogen fixation and biotechnology. *Journal of Biotechnology, 91*(2–3), 143–153.

Zaidi, A., Khan, M., Ahemad, M., & Oves, M. (2009). Plant growth promotion by phosphate solubilizing bacteria. *Acta Microbiologica et Immunologica Hungarica, 56*(3), 263–284.

Zhang, T., Hu, F., & Ma, L. (2018). Phosphate-solubilizing bacteria from safflower rhizosphere and their effect on seedling growth. *Open Life Sciences, 14*(1), 246–254.

Zhao, Y. (2010). Auxin biosynthesis and its role in plant development. *Annual Review of Plant Biology, 61*, 49–64.